

## Mechanisms and Stability of Slow Stem Rusting Resistance in *Avena sterilis*

A. Szejnberg and I. Wahl

Department of Plant Pathology, Faculty of Agriculture, The Hebrew University of Jerusalem, Rehovot, Israel. The junior author's present address: Division of Mycology, Tel-Aviv University, Tel-Aviv, Israel.

This research is a portion of the Ph.D. thesis submitted by the senior author to The Hebrew University. It was supported under P.L. 480 by the United States Department of Agriculture Grant No. PG-Is-138, A10-CR-20.

The publication is dedicated to the memory of H. C. Murphy, who discovered the slow rusting phenomenon in *Avena sterilis*, recognized its significance, and initiated this study.

The writers gratefully acknowledge the invaluable advice and assistance of L. W. Briggie, J. A. Browning, R. M. Caldwell, the late Helen Hart, H. S. Heagle, M. B. Moore, R. W. Romig, P. G. Rothman, M. D. Simons, and R. T. Smith in planning and pursuing this investigation.

Accepted for publication 10 July 1975.

### ABSTRACT

The study demonstrated that mechanisms controlling slow stem rusting in *Avena sterilis* involve restricted colonization of host tissue by mycelium, and decline in urediospore production per pustule both in seedling leaves and flag leaves of flowering plants. These factors functioned against all tested oat stem rust races, viz. 2, 8, 40, 41, and 72. The results support the concept that slow rusting is a form of general,

race-nonspecific resistance. Races with "unnecessary" genes for virulence are as fit to colonize the host and to sporulate as are races with a narrow range of virulence. The slow stem rusting resistance in *A. sterilis* was effective in field trials in Puerto Rico, the USA, and Israel.

Phytopathology 66:74-80

*Additional key words:* epidemiology, stem rust of oats, horizontal resistance, stabilizing selection.

Paucity of genes for resistance to crown rust and stem rust in cultivated oats prompted an intensive search for resistance to both diseases in the genetically diverse populations of the wild hexaploid oats species *Avena sterilis* L. This species, the putative ancestor of cultivated oats and readily crossable with them, is indigenous and widespread in Israel and other parts of the Mediterranean region (25). Our study was based on the hypothesis that resistance to both rusts has evolved in *A. sterilis* as a result of natural selection associated with a long period of host-parasite coexistence.

Local populations of *A. sterilis* constitute a rich and heterogeneous reservoir of race-specific resistance to crown rust that is expressed by infection type 1-2, and effective at all stages of plant life (25, 28). In contrast, this form of resistance to *Puccinia graminis* Pers. f. sp. *avenae* Eriks. & E. Henn. is rare in *A. sterilis*. Only 33 of 5,753 plants collected in Israel in countrywide field surveys displayed resistance associated with the above type of infection throughout their growth when inoculated with races 8, 40, and 72. Some accessions of *A. sterilis* exhibited resistance at the seedling and juvenile stages, but it declined markedly after heading (A. Szejnberg and I. Wahl, *unpublished*).

Dr. H. C. Murphy found that, in the 1967 oat stem rust nursery at Mayaguez, Puerto Rico, "Some *A. sterilis* entries [from Israel] were resistant in the seedling and juvenile stage to race 6AFH, but none retained their resistance in the adult stage. A number of the entries possessing seedling and juvenile resistance to race 6AFH [now designated race 94 (22)] were observed in the milk to soft dough stage at Mayaguez with only 10-15% susceptible type infection on the culms when our basic

sources (genes A, B, D, etc.) were killed by rust before heading. In other words, the slow-rusting entries were obviously going to produce a good yield of grain." (Letter of 2 May 1967). In a letter of 14 June 1967 Murphy wrote, "It appeared obvious that slow rusting and/or tolerance was giving significant protection in Puerto Rico last spring since many *A. sterilis* entries produced good seed. .

We obtained absolutely no seed from our basic sources of stem rust resistance among the cultivated types." Seed was harvested "from approximately 150 non-specific resistant entries" of *A. sterilis*.

Some of the promising *A. sterilis* accessions were tested in Israel from 1965 through 1968 in field plots artificially inoculated with races 8, 40, and 72. They behaved, as in Puerto Rico trials, by displaying symptoms of slow rusting protection manifested in lesser infectability of plants and slow disease spread. The uredia formed denoted susceptible host reactions.

The following mechanisms condition resistance of a similar type to other diseases: (i) reduced penetration (4, 9, 10, 15), (ii) increase of incubation period (15, 24), (iii) restricted colonization of host tissue by mycelium (4, 6, 9, 15), and (iv) decline in sporulation intensity (4, 6, 9, 10, 15, 18, 24).

The objectives of our study were to elucidate the role of the listed mechanisms in conditioning slow stem rust resistance in *A. sterilis* and to assess their effect on various races of *P. graminis avenae* infecting plants at various stages of growth. An attempt was also made to determine the degree of stability of this resistance.

**MATERIALS AND METHODS.**—*Hosts.*—*Avena sterilis* accessions AS-8 and AS-9 represented slow-rusting selections, AS-20 and AS-24 served as fast-rusting

accessions, and AS-31 supported low to intermediate levels of infection. The cultivar 'Fulghum' was used as a standard fast-rusting check and universally susceptible host for inoculum increase. The five mentioned accessions of *A. sterilis* originated from seed yielded in 1965 by plants growing in natural stands heavily attacked by stem rust. They were chosen for our studies based on their performance in the Mayaguez oat rust nursery in 1967 and in test plots in Israel in 1965-68, where they were artificially inoculated with races 2, 8, 40, 41, and 72. The race designations are those of Stewart and Roberts (22).

Race 72 was previously referred to as race 6 (23).

Germination of *A. sterilis* seed was stimulated by dehulling and placing them in petri dishes lined with moist filter paper. The treated seed was kept 4-5 days at 4 C, then at 22 C until germination started. Seed with emerging roots was planted in garden soil in 10-cm diameter clay pots. Because even vernalization does not insure uniform germination, sowing was staggered so that seedlings at nearly the same stage of development were available for inoculation. Plants were grown in the greenhouse at  $22 \pm 2$  C, periodically irrigated, and supplied with a nutrient solution. When accessions of *A. sterilis* had reached the tillering stage, six tillers were separated along with their roots from a well-developed plant and transplanted to other pots, one tiller per pot. This was the maximum number of tillers that could be successfully cloned from a single plant. Cloning was resorted to in order to increase genetic uniformity (barring somatic mutation) in plants of a species with a high rate of heterozygosity (28).

*Method of inoculation.*—Cultures of *P. graminis avenae* races 2, 8, 40, 41, and 72, of single urediospore origin, were multiplied on Fulghum seedlings. Their identity was checked periodically on differential varieties kindly provided by D. M. Stewart. Primary seedling leaves and flag leaves of flowering plants were inoculated by gently rubbing their upper surface with cotton swabs wetted with a suspension of urediospores in distilled water. Melted agar was added to the suspension at the rate of 0.1% to improve spore retention on the foliage. Prior to inoculation, the foliage was sprayed with a 0.05% solution of Tween-20 (polyoxyethylene sorbitan monolaurate). Each plant was inoculated with one race only. The inoculated plants were maintained 24 hours in  $21 \pm 2$  C water-saturated growth chambers and subsequently grown in  $22 \pm 2$  C greenhouses. Adult plant tests were performed with clones. Each clone in a replication was derived from a different plant, and was matched by its sister clones in the remaining replications.

*Penetration.*—Primary seedling leaves and flag leaves of flowering plants of accessions AS-8, AS-9, AS-20, and AS-24 were inoculated with races 2, 8, 40, 41, and 72, each plant with a single race. Study of the penetration rate of the fungus during the first 48 hours after inoculation, involved 50 seedling leaves and 50 leaves from adult plants of each accession. They were divided into five groups. Each group comprised 10 leaves that had previously been inoculated with the same race. The detached leaves were immersed immediately in a solution of alcohol-lactophenol-cotton blue and processed using the whole-leaf clearing and staining technique of Shipton and Brown (19). Upon treatment, leaf segments were mounted under a cover glass in a drop of 50% glycerol on microscopic slides and examined at  $\times 250$  magnification. About 30 appressoria were examined on each leaf. The rate of successful penetration was measured by evaluation of the percentage of appressoria that developed substomatal vesicles producing infection hyphae (9, 14).

*Incubation period.*—Definitions of disease incubation period are conflicting. In this study the concept was adopted which considers "for practical purposes... the period of incubation... the time between inoculation and sporulation" (21).

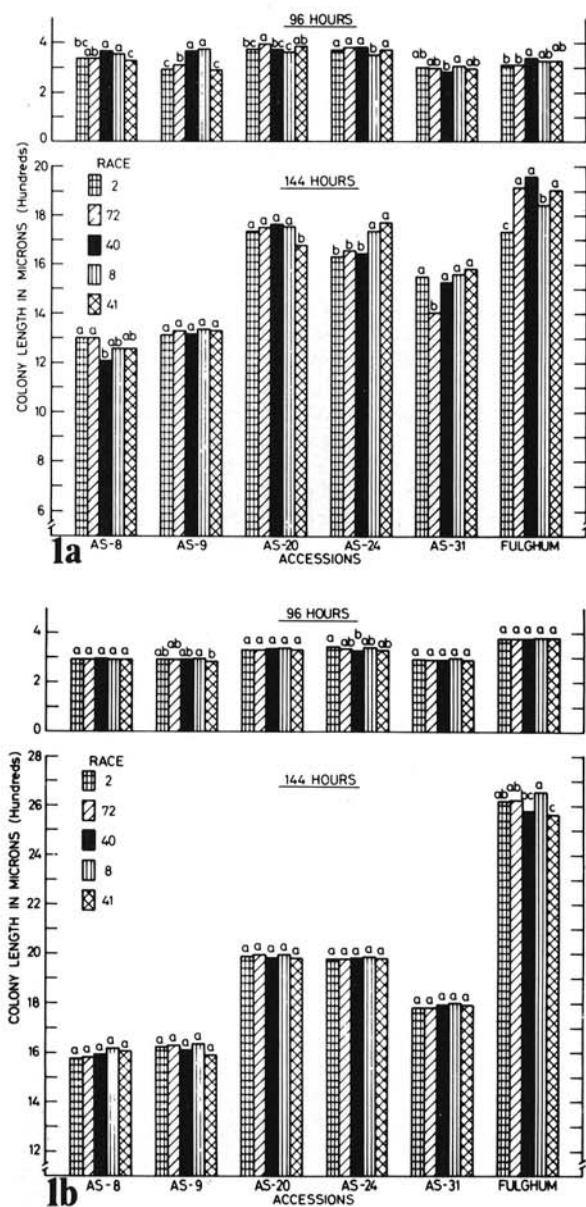


Fig. 1.—(a, b). Average colony length produced by the specified races of *Puccinia graminis avenae* on a) primary leaves, and on b) flag leaves at flowering stage of the indicated oat accessions 96 and 144 hours after inoculation. Different letters are assigned to means which are significantly different at  $P = 0.05$ .

*Mycelium development.*—The ability of hyphae to colonize the host was studied in primary leaves and in flag leaves of flowering plants in the mentioned accessions of *A. sterilis* and Fulghum. The inoculation, incubation, and staining procedures were the same as in the fungus penetration study. The hyphal extension was assessed with an ocular micrometer ( $\times 250$ ). To determine the rate of mycelial growth from a single infection site, the distance was measured between the tips of the most extended hyphae microscopically visible at the opposite ends of the colony (6, 9). Only the growth progress of hyphae parallel to the long axis of the leaf was studied since hyphal growth in other directions was limited by veins 48-72 hours after inoculation. The colony increase was estimated 48, 96, and 144 hours after inoculation. The length of 90 colonies on nine leaves was measured for each race on each accession for both seedling and flag leaves. The results were submitted to analysis of variance and multiple range test.

*Urediospore production.*—We investigated the urediospore yielding capacity of the stem rust races in primary leaves and in flag leaves of flowering plants of our oat accessions using the method of Heagle and Moore (9). The inoculation and incubation procedures were as in previous trials. To determine the rate of urediospore production by a single pustule, leaves with a similar number of flecks were placed in flexible, translucent plastic troughs, one leaf blade per trough (9). The blades were held on edge by small pins inserted into the trough base on both sides of the leaf. In seedling tests the troughs were 15 to 20 cm long and 1.5 cm in diameter with a 1 cm open space running down the top. In adult plant experiments the troughs were 20 to 30 cm long, 2.5 cm in diameter, with edges 2 cm apart. This arrangement made possible escape of excessive moisture and accessibility to the leaf blade. The troughs rested on supports sloped slightly away from the plant toward the exit to permit spore collection. Urediospores were washed from the leaves to glass vials with a 0.05% Tween-20 solution in distilled water released under low pressure from plastic bottles connected to an air pump. Subsequently, the blades were rinsed with distilled water. A few drops of cotton blue solution were added to the urediospore suspension to facilitate counting. Spores were collected at 3-day intervals, starting 10 days after inoculation, seven times in succession for seedling leaves, and 11 times for flag leaves. The spore suspension was homogenized 30 minutes with a magnetic stirrer. The number of spores in five samples for each collection was counted on a hemacytometer. Spore yield per uredium was calculated by dividing the total number of spores collected in each treatment by the number of functioning pustules. The number of uredia per blade increased during the experiment; therefore, the number of pustules yielding spores at a given collection was calculated as the mean number of uredia counted at the current and preceding collection for each replication. The results were submitted to analysis of variance and multiple range test. Tests with seedling leaves were run in four replications. Each replication involved accessions AS-8, AS-9, AS-20, AS-24, AS-31, and Fulghum, and comprised a total of 150 seedlings, 25 seedlings per accession. The 25 seedlings were divided into five groups of five plants, and plants of each group were inoculated with one of the tested races.

Tests with flag leaves were conducted in five replications. In each replication blades of two leaves of every accession were inoculated with one of the five races.

**RESULTS.—Penetration.**—The rate of penetration was the same for all races on all leaves, averaging 55% on seedlings and 45% on flag leaves.

*Incubation period.*—The duration of the disease incubation period was the same for accessions AS-8, AS-9, AS-20, AS-24, AS-31, and Fulghum, regardless of the race implicated in infection. This process lasted 7.5-8 days in seedlings and 8-8.5 days in flag leaves at  $22 \pm 2$  C.

*Mycelium development.*—The hyphal growth of all races was rather uniform within 48 hours after inoculation for all five races in both primary leaves and flag leaves in all accessions. The length of the mycelial mat ranged from 57 to 67  $\mu$ m. About 96 hours after inoculation significant differences in the colony size of some races were noticed in seedlings of most accessions (Fig. 1-a). The sequence of colony ratings varied with the particular accession used for inoculation. For example, race 40 formed the largest colonies in AS-8, AS-24, and Fulghum, but the smallest ones in AS-31 (Fig. 1-a). The colony lengths in the accessions involved varied in the range of 282 to 393  $\mu$ m.

In flag leaves the colony length was rather uniform in plants of a given accession. Unlike in seedlings, clear distinctions in colony lengths were recorded among flag leaves of three groups of accessions (Fig. 1-a, 1-b). The mean colony lengths varied from 283 to 296  $\mu$ m in group AS-8, AS-9, and AS-31; from 325 to 333  $\mu$ m in group AS-20, AS-24; and was 375  $\mu$ m in Fulghum (Fig. 1-b).

The intensity of hyphal development gained momentum during the period of 96 to 144 hours after inoculation (Fig. 1-a, 1-b). This was especially evident in flag leaves of Fulghum and to a lesser degree in the primary and flag leaves of other oat entries. Hyphal growth of all races was rather uniform in flag leaves of all accessions, while in seedlings some degree of variability was obvious. In seedling leaves, as in flag leaves, the colonization process was distinctly less vigorous in slow-rusting accessions AS-8, AS-9, and AS-31 than in fast-rusting accessions AS-20, AS-24, and Fulghum. This was reflected in the average colony lengths which in flag leaves ranged from 1576 to 1633  $\mu$ m in the AS-8, AS-9 group; was 1790  $\mu$ m in AS-31; varied from 1976 to 1992  $\mu$ m in the AS-20, AS-24 group; and reached 2655  $\mu$ m in Fulghum (Fig. 1-b).

*Urediospore production.*—Fig. 2-a and 2-b depict the cumulative urediospore yields per pustule at the indicated collection dates on primary leaves and flag leaves of the tested accessions. They were calculated by adding yields of all preceding collections of the respective race on the specified host to the current spore harvest.

In the seedling trials the following results were obtained. In race 2, which is common in Israel and characterized by a limited range of virulence, the mean cumulative number of spores per pustule was, after seven collections: 51,000 on Fulghum, 21,000 on AS-31, 32,500 on AS-24, 31,000 on AS-20, 21,500 on AS-9, and 21,000 on AS-8.

In the predominant race 72, with a wide range of virulence (23), the average cumulative number of spores per uredium was, after seven collections: 47,500 on Fulghum, 21,000 on AS-31, 34,000 on AS-24, 32,000 on

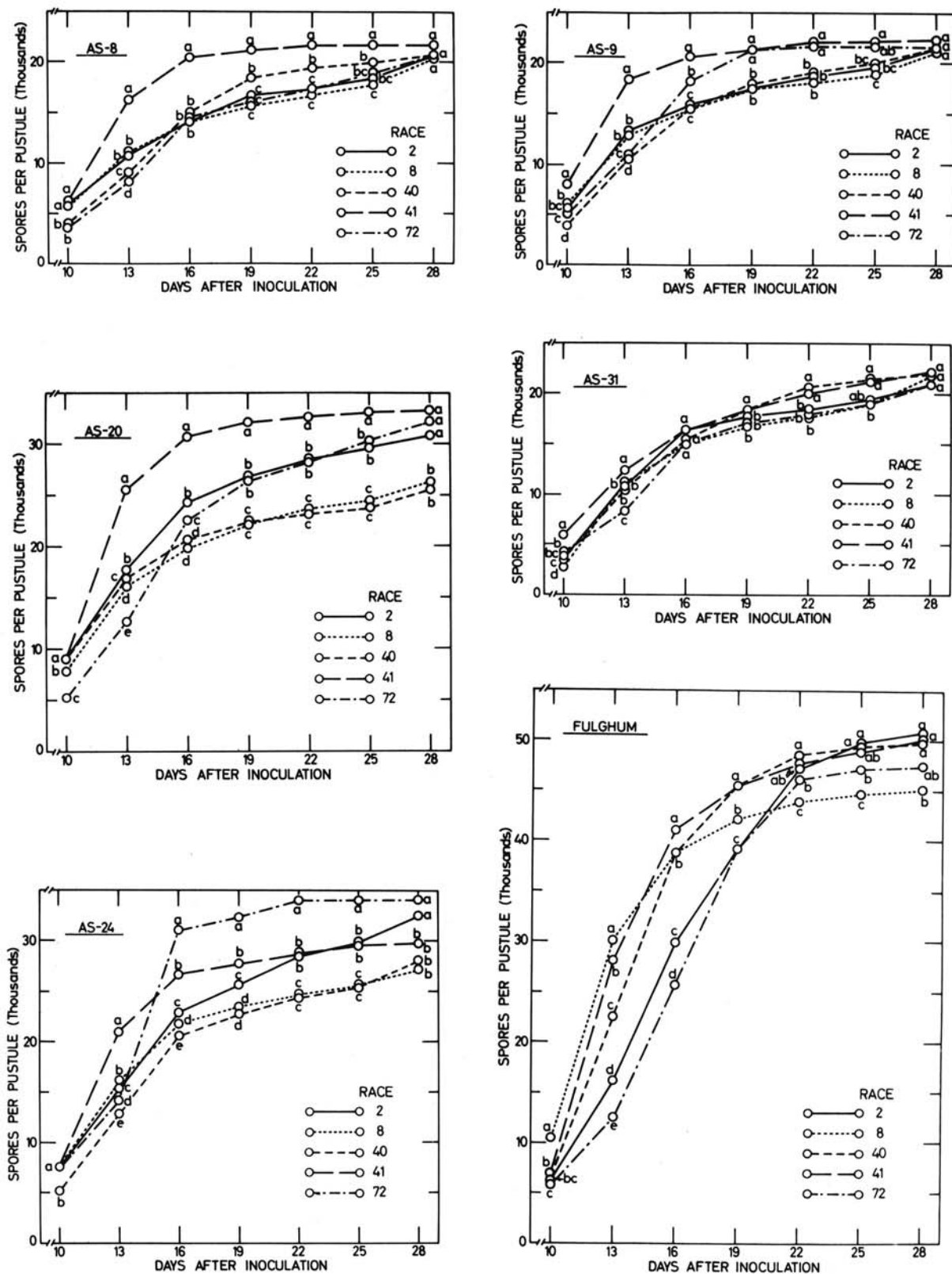


Fig. 2-a. Average cumulative number of spores per uredium produced by the specified races of *Puccinia graminis avenae* on primary leaves of the indicated oat accessions. Different letters are assigned to means significantly different at  $P = 0.05$ .

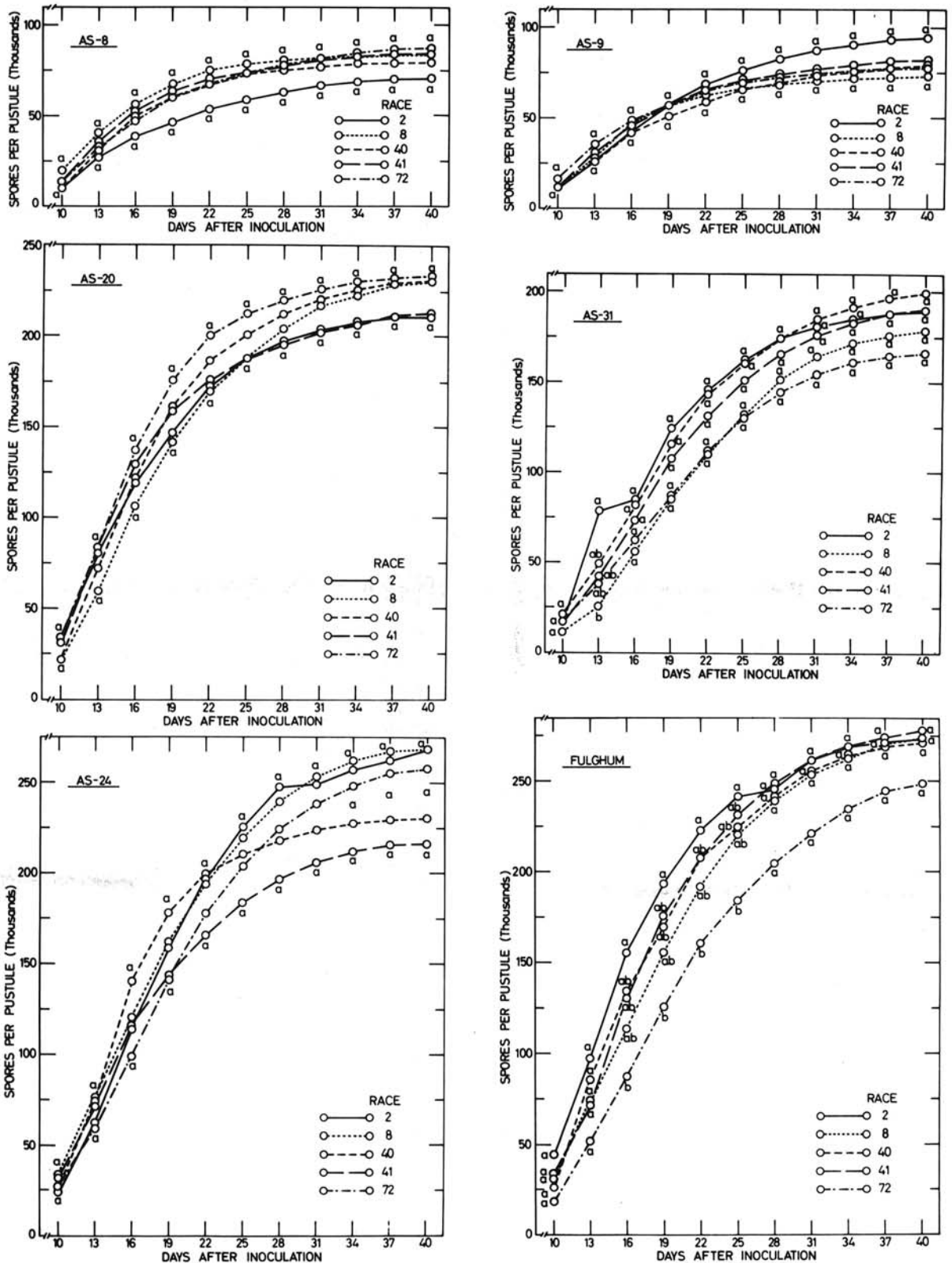


Fig. 2-b. Average cumulative number of spores per uredium produced by the specified races of *Puccinia graminis avenae* on flag leaves of the indicated oat accessions. Different letters are assigned to means significantly different at  $P = 0.05$ .

AS-20, 22,000 on AS-9, and 21,000 on AS-8.

In the rare race 41, with the broadest spectrum of virulence (23), the mean cumulative number of spores per uredium amounted, after seven collections, to: 50,000 on Fulghum, 22,000 on AS-31, 30,000 on AS-24, 33,000 on AS-20, 22,000 on AS-9, and 22,000 on AS-8.

Similar differentiation in spore productivity on the accessions concerned were evident in races 8 and 40. Obviously, the sporulation intensity of all races was alike and relatively low on the slow-rusting AS-8, AS-9, and AS-31, and distinctly higher on the fast-rusting AS-20, AS-24, and Fulghum (Fig. 2-a).

In tests with flag leaves the sporulation intensity of each race varied with the accession and showed the same trends as in seedling trials. Deviations in sporulation prolificacy on the infected accessions were small in the first two collections, becoming more pronounced with the progress of the experiment. The accessions could be divided into three groups on the basis of the cumulative spore counts per uredium. Their ranking followed the same order for all races (Fig. 2-b). The most abundant sporulation was recorded on Fulghum, AS-24, and AS-20; the lowest yields were produced on AS-8 and AS-9; while on AS-31 an intermediate level of sporulation was attained. The sequence of sporulation ratings on accessions within a group occasionally varied with the race, or with the progress of the experiment with the same race. The cumulative number of urediospores per pustule after 11 collections averaged on Fulghum, AS-31, AS-24, AS-20, AS-9, and AS-8, respectively (in thousands): for race 2 - 270, 189, 268, 211, 94, and 71; for race 8 - 273, 179, 269, 230, 73, and 83; for race 72 - 248, 166, 258, 234, 78, and 87; for race 40-271, 200, 230, 231, 78, and 79; for race 41 - 278, 190, 216, 213, 82, and 84.

Clearly, patterns of urediospore productivity of all races were similar on flag leaves of any one of the tested oat accessions, but varied significantly among the accessions. Each race yielded about three times as many urediospores per pustule on AS-24 or AS-20, and over twice as many on AS-31, as on AS-9 or AS-8.

The spore yield of a race was often influenced by the host and its age. For example, race 2 outranked in prolificacy other races on flag leaves of Fulghum and AS-9, but was least productive on AS-8. This race never excelled on seedlings of any accession. Race 41, in contrast, surpassed other races in fertility on seedlings of AS-8, AS-9, and AS-20, and for limited time periods also on Fulghum and AS-31, but was not an outstanding producer on flag leaves.

Ordinarily, sporulation intensity peaked during the first half of a test, declining with the senescence of the leaf. All uredia formed throughout the study were of the infection type 3-4.

*Stability of slow stem rusting resistance.*—Studies with numerous accessions of *A. sterilis* conducted under a wide range of environment and exposed to a broad spectrum of races attest to the stability of the slow stem rusting type of resistance. Accessions AS-8 and AS-9 rusted slowly in test nurseries in Israel from 1965 to 1968, infected with races 2, 8, 40, 41, and 72. In Iowa, plants of AS-8 and AS-9 remained green until maturity, whereas oat cultivars endowed with common major stem rust resistance genes were killed by race 31 (2). Similar results were obtained in experiments conducted with these accessions and with the

same race at the University of Minnesota, St. Paul, by the junior author jointly with M. B. Moore, R. W. Romig, and P. G. Rothman (*unpublished*). In Israel, in field plots infected with races 2, 8, 40, and 72, slow development of stem rust was recorded on accessions AS-8 and AS-9 annually, from 1969 through 1975 (J. Manistersky and I. Wahl, *unpublished*).

**DISCUSSION.**—Slow rusting, expressed in reduced infectability of a plant by a rust fungus, late appearance of the rust in the life of the host, and retarded development of the fungus, is considered to be a form of general, race non-specific resistance (4, 10, 13, 20). It was described in oats attacked by crown rust (13, 20), wheat stricken by leaf rust (5) or stem rust (26), and referred to as slow rusting. The same type of protection has been observed on wheat cultivars infected with powdery mildew and termed slow mildewing (16, 18).

H. C. Murphy postulated that, "the slow rusting exhibited by *A. sterilis* to [race] 6AFH in Puerto Rico should give adequate protection under field conditions to all races without exerting any screening effect on the race populations" (letter of 29 May 1967). This concept of race-nonspecificity of slow rusting resistance gained support in our study. Decreased colonization and reduced sporulation, the two mechanisms involved in slow stem rusting of *A. sterilis*, proved effective regardless of the race parasitizing the host.

The relative commonness of the race-specific resistance to crown rust in adult plants of *A. sterilis* is sharply contrasted by the rarity of this type of protection to stem rust. The reasons for this phenomenon are being investigated. The relatively common occurrence of the general type of resistance to stem rust in *A. sterilis* supports Zhukovsky's hypothesis (27) that the wild relatives of cultivated plants in the centers of their origin are, as a rule, protected from their parasites by mechanisms of tolerance or "field resistance" that are characterized by reduced infectability of the host and restricted sporulation of the pathogen.

By diminishing the spore load of *P. graminis avenae*, the slow-rusting type of resistance mitigates stem rust epidemics in oat fields and minimizes depletion of energy in the infected host. The saved energy enhances yield production (8). This may explain why slow-rusting accessions of *A. sterilis* set good quality seed while the fast-rusting plant yielded absolutely no seed in the same field plots.

Incorporation of lasting resistance of the slow-rusting type into cultivated oats is particularly important in view of the ephemerality of race specific resistance to *P. graminis avenae* (3, 24). Resgenes most promising some years ago proved ineffective in recent studies (17).

Results of our study support the concept that slow rusting is a form of general resistance. Nevertheless, more research is needed to test the validity of this supposition, particularly in view of evidence that seems to contest it in the case of leaf rust of wheat (1).

It also remains to be seen if slow rusting will contribute to solving "the basic and most difficult problem of preserving disease resistance for long periods of time in varieties under mass cultivation" (7).

In contrast to the scarcity of cultivated oats in Israel, *A. sterilis* is ubiquitous, forming large and lush stands that are attacked annually by stem rust. This situation offers

an opportunity to study the evolution of race populations of *P. graminis avenae* in the center of origin of *A. sterilis*, under natural conditions, exposed to natural selection, and not "man-guided" (11). Race 72 has predominated in Israel for many years (23). Its prevalence cannot be ascribed to the preferential selection pressure of the host, and shows that a race with a wide range of virulence is not inferior in fitness to survive and to compete even when its virulence is "unnecessary," as postulated by some researchers (12, 24). Race 72 predominates over races 40 and 41 with more virulences and over races 8 and 2, which possess fewer unnecessary virulences. A similar situation exists in crown rust on *A. sterilis* (25).

Our results also reveal that virulence of an oat stem rust race does not influence its ability to penetrate the host, to colonize the plant tissue, and to produce inoculum. The possibility is being investigated that factors other than virulence, such as ecologic conditions (3), determine the composition of stem rust races populations on *A. sterilis*.

#### LITERATURE CITED

- BROWDER, L. E. 1973. Specificity of the *Puccinia recondita* f. sp. *tritici*: *Triticum aestivum* 'Bulgaria 88' relationship. *Phytopathology* 63:524-528.
- BROWNING, J. A. 1973. Oats: A continental control program. Pages 155-180 in R. R. Nelson, ed. *Breeding plants for disease resistance*. Pennsylvania State Univ. Press. University Park. 401 p.
- BROWNING, J. A., and K. J. FREY. 1969. Multiline cultivars as a means of disease control. *Annu. Rev. Phytopathol.* 7:355-382.
- CALDWELL, R. M. 1968. Breeding for general and/or specific plant disease resistance. Pages 263-272 in K. W. Finlay, and K. W. Shepherd, eds. *Proc. 3rd Int. Wheat Genet. Symp., Austr. Acad. Sci. Canberra*. 479 p.
- CALDWELL, R. M., J. J. ROBERTS, and Z. EYAL. 1970. General resistance ("slow rusting") to *Puccinia recondita* f. sp. *tritici* in winter and spring wheats. *Phytopathology* 60:1287 (Abstr.).
- CLIFFORD, B. C. 1972. The histology of race non-specific resistance to *Puccinia hordei* Otth in barley. Pages 75-78 in *Proc. European and Mediterranean. Cereal Rusts Conference I, Prague*. 307 p.
- DUNIN, M. S. 1959. Preface to the Russian edition of E. C. Stakman's and J. G. Harrar's book, *Principles of plant pathology (Osnovy patologii rastenii)*. Published by Innostrannoi literatury. Moscow. 540 p.
- FREY, K. J., J. A. BROWNING, and M. D. SIMONS. 1973. Management of host resistance genes to control diseases. *Z. Pflanzenkrankh. Pflanzenschutz* 80:160-180.
- HEAGLE, A. S., and M. B. MOORE. 1970. Some effects of moderate adult resistance to crown rust of oats. *Phytopathology* 60:461-466.
- HOOKER, A. L. 1967. The genetics and expression of resistance in plants to rusts of the genus *Puccinia*. *Annu. Rev. Phytopathol.* 5:163-182.
- JOHNSON, T. 1961. Man-guided evolution in plant rusts. *Science* 133:357-362.
- LEONARD, K. J. 1969. Selection in heterogeneous populations of *Puccinia graminis* f. sp. *avenae*. *Phytopathology* 59:1851-1857.
- LUKE, H. H., R. D. BARNETT, and W. H. CHAPMAN. 1975. Types of horizontal resistance of oats to crown rust. *Plant Dis. Rep.* 59:332-334.
- MAHESHWARI, R., P. J. ALLEN, and A. C. HILDEBRANDT. 1967. Physical and chemical factors controlling the development of infection structures from urediospore germ tubes of rust fungi. *Phytopathology* 57:855-862.
- NELSON, R. R. 1973. The use of resistance genes to curb population shifts in plant pathogens. Pages 49-66 in R. R. Nelson, ed. *Breeding plants for disease resistance*. Pennsylvania State Univ. Press. University Park. 401 p.
- ROBERTS, J. J., and R. M. CALDWELL. 1970. General resistance (slow mildewing) to *Erysiphe graminis* f. sp. *tritici* in Knox wheat. *Phytopathology* 60:1310 (Abstr.).
- ROELFS, A. P., and P. G. ROTHMAN. 1974. Races of *Puccinia graminis* f. sp. *avenae* in the U.S.A. during 1973. *Plant Dis. Rep.* 58:605-607.
- SHANER, G. 1973. Reduced infectability and inoculum production as factors of slow mildewing in Knox wheat. *Phytopathology* 63:1307-1311.
- SHIPTON, W. A., and J. F. BROWN. 1962. A whole-leaf clearing and staining technique to demonstrate host-pathogen relationships of wheat stem rust. *Phytopathology* 52:1313.
- SINGLETON, L. L., and M. B. MOORE. 1973. Evaluation of selected nonspecific resistance characters of some oat lines for reducing yield losses caused by *Puccinia coronata* var. *avenae*. Abstract No. 0631 in *Abstracts of Papers, 2nd Int. Congr. Plant Pathol., 5-12 Sept., Minneapolis, Minnesota*. (unpaged).
- STAKMAN, E. C., and J. G. HARRAR. 1957. *Principles of plant pathology*. Ronald Press, New York. 581 p.
- STEWART, D. M., and B. J. ROBERTS. 1970. Identifying races of *Puccinia graminis* f. sp. *avenae*. *U. S. Dep. Agric., Tech. Bull.* 1416. 23 p.
- SZTEJNBERG, A., and I. WAHL. 1967. A new and highly virulent race of oat stem rust in Israel. *Plant Dis. Rep.* 51:967-970.
- VAN DER PLANK, J. E. 1968. *Disease resistance in plants*. Academic Press, New York and London. 206 p.
- WAHL, I. 1970. Prevalence and geographic distribution of resistance to crown rust in *Avena sterilis*. *Phytopathology* 60:746-749.
- WILCOXSON, R. D., A. H. ATIF, and B. SKOVMAND. 1974. Slow rusting of wheat varieties in the field correlated with stem rust severity on detached leaves in the greenhouse. *Plant Dis. Rep.* 58:1085-1087.
- ZHUKOVSKY, P. M. 1959. Vzaimootnoshennia mezhdru khozinom i gribnym parazitom na ikh rodine i vne ee (Interrelation between host and parasite in their origin and beyond it). *Vestnik sel'skokhoziaistvennoi nauki* 4(6):25-34 (Russian, with English summary).
- ZILLINSKY, F. J., and H. C. MURPHY. 1967. Wild oat species as sources of disease resistance for the improvement of cultivated oats. *Plant Dis. Rep.* 51:391-395.